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Review

A review of the phylogeny, ecology and toxin production of bloom-forming *Aphanizomenon* spp. and related species within the Nostocales (cyanobacteria)

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A B S T R A C T

The traditional genus *Aphanizomenon* comprises a group of filamentous nitrogen-fixing cyanobacteria of which several memebers are able to develop blooms and to produce toxic metabolites (cyanotoxins), including hepatotoxins (microcystins), neurotoxins (anatoxins and saxitoxins) and cytotoxins (cylindrospermopsin). This genus, representing geographically widespread and extensively studied cyanobacteria, is in fact heterogeneous and composed of at least five phylogenetically distant groups (*Aphanizomenon*, *Anabaena*/*Aphanizomenon* like cluster A, *Cuspidothrix*, *Sphaerospermopsis* and *Chrysosporum*) whose taxonomy is still under revision. This review provides a thorough insight into the phylogeny, ecology, biogeography and toxicogenomics (cyr, sxt, and ana genes) of the five best documented "*Aphanizomenon*" species with special relevance for water risk assessment: *Aphanizomenon flos-aquae*, *Aphanizomenon gracile*, *Cuspidothrix issatschenkoi*, *Sphaerospermopsis aphanizomenoides* and *Chrysosporum ovalisporum*. *Aph. flos-aquae*, *Aph. gracile* and *C. issatschenkoi* have been reported from temperate areas only whereas *S. aphanizomenoides* shows the widest distribution from the tropics to temperate areas. *Ch. ovalisporum* is found in tropical, subtropical and Mediterranean areas. While all five species show moderate growth rates (0.1–0.4 day^{-1}) within a wide range of temperatures (15–30 °C), *Aph. gracile* and *A. flos-aquae* can grow from around (or below) 10 °C, whereas *Ch. ovalisporum* and *S. aphanizomenoides* are much better competitors at high temperatures over 30 °C or even close to 35 °C. *A. gracile* has been confirmed as the producer of saxitoxins and cylindrospermopsin, *C. issatschenkoi* of anatoxins and saxitoxins and *Ch. ovalisporum* of cylindrospermopsin. The suspected cylindrospermopsin or anatoxin-a production of *A. flos-aquae* or microcystin production of *S. aphanizomenoides* is still uncertain. This review includes a critical discussion on the the reliability of toxicity reports and on the invasive potential of "*Aphanizomenon*" species in a climate change scenario, together with derived knowledge gaps and research needs. As a whole, this work is intended to represent a key reference for scientists and water managers involved in the major challenges of identifying, preventing and mitigating toxic *Aphanizomenon* blooms.

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1. Introduction

Worldwide, agricultural, urban and industrial activities have caused a nutrient over-enrichment in many freshwater ecosystems, leading to the phenomenon of periodic blooms of prokaryotic cyanobacteria (Paerl and Huisman, 2009). Many cyanobacteria can produce hepatotoxic and neurotoxic cyanobacterial secondary metabolites which can cause serious chronic human and acute animal health problems, or in some cases even mortalities (Carmichael, 2001; Paerl and Huisman, 2009). Therefore, the use of surface waters for irrigation, drinking water and recreational purposes is often limited by the presence of cyanobacteria, cyanobacterial toxins or other secondary metabolites (Hitzfeld et al., 2000; Carmichael, 2001; Saqrane and Oudra, 2009).

Cyanobacteria belonging to the orders Chroococcales, Oscillatoriales or Nostocales can be involved in such blooms and species belonging to all orders are known as potential producers of cyanobacterial toxins (Codd et al., 1999).

The genus *Aphanizomenon* belongs to the order Nostocales and several of its members have been described as the cause for harmful blooms since the end of the 19th century (Nelson, 1903; Codd et al., 1999). The genus *Aphanizomenon* has been traditionally defined by its morphological characteristics, comprising planktonic cyanobacteria with more or less straight trichomes and which occur as single filaments or have a tendency to form fascicles. As in most planktonic and potential bloom-forming cyanobacteria, vegetative cells of *Aphanizomenon* often contain gas vesicles providing buoyancy under certain environmental conditions. Apical cells in the trichomes are not (or slightly) narrowed towards ends, with elongated and partially or totally hyaline apical cells. Nevertheless, recent studies using a polyphasic approach – involving not only morphology but also ecology and phylogenetics – have revealed that the traditional genus *Aphanizomenon* is in reality very heterogeneous. The newly defined genus *Aphanizomenon* has accordingly been restricted to a well-defined cluster of eight morphospecies (e.g. *Aphanizomenon flos-aquae* Ralfs ex Bornet & Flahault) (Lyra et al., 2001; Gugger et al., 2002; Rajaniemi et al., 2005a,b; Komárek and Komárková, 2006; Komárek, 2013). Several members of the former traditional genus *Aphanizomenon* which are characterized by growth with single straight filaments have been assigned to the new genera *Cuspidothrix* (e.g., former *Aphanizomenon issatschenkoi* (Usačev) Proshkina-Lavrenko), *Sphaerospermopsis* (e.g., former *Aphanizomenon aphanizomenoides* (Forti) Hortobágyi & Komárek) or *Chrysosporum* (e.g., former *Aphanizomenon ovalisporum* Forti) or to *Anabaena/Aphanizomenon* like (e.g. *Aphanizomenon gracile* (Lemmermann) Lemmermann) or *Anabaena*-like groups (Rajaniemi et al., 2005b; Zapomělová et al., 2009, 2010; Komárek, 2013).

A variety of cyanobacterial species assigned to the traditional genus *Aphanizomenon* have been described to produce a variety of cyanotoxins with hepatoxic, neurotoxic and cytotoxic effects in mammals (Sivonen et al., 1989; Preussel et al., 2006; Wood et al., 2007; Ballot et al., 2010a; Kokociński et al., 2013). Despite this potential toxin production, the biomass of some *Aphanizomenon* populations (namely *Aphanizomenon flos-aquae*) mixed with co-occurring cyanobacterial taxa is harvested for health-food supplements with the consequent risks for consumers health (Carmichael et al., 2000; Saker et al., 2005; Grewe and Pulz, 2012).

This review presents the state of the art of the morphology, phylogenetics, toxin production, ecology and biogeography of members of the traditional genus "*Aphanizomenon*". It focuses mainly on those "*Aphanizomenon*" species of which morphological, genetic and toxin data are available: *Aphanizomenon flos-aquae*, *Aphanizomenon gracile*, *Cuspidothrix issatschenkoi* (Usachev) Rajaniemi, Komárek, Willame, Hrouzek, Kastovská, Hoffmann & Sivonen (formerly *Aphanizomenon issatschenkoi*), *Chrysosporum ovalisporum* (Forti) Zapomělová, Skácelová, Pumann, Kopp & Janecek (formerly *Aphanizomenon ovalisporum*) and *Sphaerospermopsis aphanizomenoides* (Forti) Zapomělová, Jezberová, Hrouzek, Hisem, Reháková & Komárková (formerly *Aphanizomenon aphanizomenoides*). Other *Aphanizomenon* species are discussed when relevant. Many studies have confused the species *Aph. flos-aquae* and *Aph. gracile* which, using morphological criteria, are now assigned to the new genus *Aphanizomenon* and to an *Anabaena/Aphanizomenon*-like cluster A, respectively. *Aph. flos-aquae* and *Aph. gracile* and closely related species are therefore discussed in one main section (Section 2.1.1). Potentially toxic species assigned to the new genera *Chrysosporum*, *Cuspidothrix* and *Sphaerospermopsis* are discussed in separated sections (Sections 2.1.2–2.1.4).